



Airborne LiDAR reveals context dependence in the effects of canopy architecture on arthropod diversity



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ABSTRACT

Ecologists have long recognized the important role of canopy heterogeneity in structuring the diversity of animal communities. However, studies directly linking variation in the three-dimensional structure of forests to variation in biodiversity are still rare. For canopy arthropods representing a dominant component of forest biodiversity in montane spruce forests of Europe, we used publicly available airborne LiDAR measurements to test the premises of two existing hypotheses that resource concentration and habitat heterogeneity are potential drivers of faunal diversity at both the tree scale and stand scale. We sampled 391 arthropod species from the canopies of 60 trees; coverage-based rarefaction revealed high completeness of faunal sampling (93.7%). When we controlled for elevation and broadleaf tree cover, we found strong (tree and stand scale) context dependence in the response of arthropod diversity to variation in vegetation structure. Arthropod diversity increased with increasing canopy density at the tree scale and was positively associated only with vegetation heterogeneity at the tree scale, but decreased with increasing canopy density at the stand scale. These trends held across all levels of biological response from total richness to diversity measures to richness of different guilds. Our results showed that different components of vegetation structural complexity drive canopy arthropod biodiversity at different spatial scales. Highest canopy arthropod diversity can be expected in spruce forests with relatively open stands containing individual trees with dense and long crowns. Thus, LiDAR opens new avenues for testing ecological hypotheses and for forest-growth models to be linked with the canopy diversity of forests.

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1. Introduction

Understanding the factors that shape the distribution and diversity of organisms is one of the central goals in ecology (Gaston, 2000). For forest ecologists, the seminal work of the MacArthur and MacArthur (1961) linking the three-dimensional heterogeneity of canopy vegetation structure to variation in bird species diversity represented one of the most important conceptual advances in understanding how variation in canopy architecture could shape animal biodiversity. Since that time, however, relatively few empirical studies have explored the role of canopy architecture in shaping species distribution patterns in taxa other than birds (Hijii et al., 2001).

This is surprising, as the last 50 years have seen a revolution in our understanding of forest canopy biodiversity, particularly for canopy arthropods (Stork et al., 1997; Basset et al., 2003; Floren and Schmidl, 2008). However, a large proportion of these studies have focused either implicitly or explicitly on the vertical stratification of assemblages from ground to canopy (e.g., Stork et al., 1997; Mitchell et al., 2002; Floren and Schmidl, 2008) but not on the direct correlation between species diversity and canopy structure. Such studies have been restricted to a comparatively narrow range of vertebrates (Bradbury et al., 2005; Jung et al., 2012) or invertebrate taxa (Halaj et al., 2000; Tanabe, 2002). In canopy diversity studies, relatively little effort has gone into overcoming the logistical hurdles surrounding cost-effective measurement of canopy architecture.

The advent of high-resolution remote-sensing techniques, such as airborne LiDAR, can now meet this challenge and provide precise data on canopy structure at high grain resolution over more or less any large spatial extents. These techniques have been well

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proven to provide accurate growing stock and foliage distribution statistics (Nelson et al., 1988; Goetz et al., 2007; Clawges et al., 2008). Here foliage, stems, branches and twigs form the major vegetation surface in a forest. Therefore the number of returns from this surface is a useful proxy for resource density for most above ground organisms (e.g., Greenstone, 1984), while vegetation heterogeneity is one prominent proxy for habitat heterogeneity in forests (Tews et al., 2004).

Canopy architecture can affect arthropods directly via tree structural complexity, or indirectly via plant species composition and corresponding differences in microclimatic conditions, plant texture of individual species and distribution of leaf quality for phytophagous consumers (Didham and Fagan, 2004; Ishii et al., 2004; Ulyshen, 2011). The problem is that many of these factors can be highly intercorrelated and can change in concert with differences in factors such as tree age and size, or even stand size at the landscape scale. In general, it is well known that species richness increases with increasing habitat area or ecosystem size owing to several underlying ecological processes (Post et al., 2000; Peay et al., 2007; Blakely and Didham, 2010). In the context of canopy arthropod diversity studies, two of the most relevant hypotheses are that (1) larger ecosystems, such as large canopy volumes (representing the summed surface area of leaves, twigs, branches and stems), are likely to contain a higher density of resources (per unit volume; e.g., foliage, sugar, wood, epiphytes, prey, and hosts; Ulyshen, 2011) with higher productivity (*resource concentration hypothesis*), and at the same time (2) could have higher variability in structure (e.g., branching pattern, distribution of leaf area and open space; Tews et al., 2004), thus providing more niches for more, different species (*habitat heterogeneity hypothesis*). In real-world situations, discriminating between such concealed hypotheses is often challenging (Blakely and Didham, 2010).

Moreover, the heterogeneity of an environment may vary with the perspective of a species. Small species might be expected to perceive and respond to the world at very fine scales, such that habitat surfaces will appear much more rugose for these species than for larger species that respond at a coarser scale. Plant surfaces in particular have been identified as habitats with high fractal dimension (Morse et al., 1985), and therefore one might expect that small species will be more influenced by habitat variation at the finer within-tree scale than at the larger stand-level scale. Context dependence, in the sense of environmental variables measured at different scales around an observation plot, has been widely observed in ecological patterns and processes, e.g., in local communities of birds (Seavy et al., 2009) and of arthropods (Steffan-Dewenter et al., 2002). For such studies, airborne LiDAR provides the opportunity for researchers to select the scale of choice at a resolution never before possible in complex forests. For ecologists and managers working at multiple spatial scales, typically at the tree scale vs. stand scale in forest production systems (Pretzsch and Schütze, 2005), or at the local vs. patch vs. landscape scales in landscape ecology (Didham et al., 2012), this would allow investigation of whether mechanisms driving community assembly and turnover across spatial scales demonstrate context dependency (Barton et al., *in press*). Here we focused on the impact of variables classified at the direct surrounding of a tree and the forest stand in which a tree grows.

In general, Europe has progressed in understanding some key structural variables for the conservation of biodiversity in forests (such as veteran trees and dead wood) and in understanding the importance of mixed tree composition and the influence of canopy density on arthropod diversity at the ground level (Bauhus et al., 2009; Sobek et al., 2009; Müller and Büttler, 2010; Vierling et al., 2011). Furthermore, various measures of stand structural heterogeneity have been proposed for guiding management (Solomon

and Grove, 1999; Pretzsch, 2002). However, any effects of variation in tree crown architecture beyond wood quality and tree stability, such as effects on biodiversity, are still poorly understood (Pretzsch, 2002).

Nowadays, commercial spruce (*Picea abies*) forests are the most widespread forest type in Central Europe, with a particular dominance in montane areas (Röder et al., 2010). In our study presented here, we directly correlated airborne LiDAR data with the diversity of spruce canopy arthropod assemblages, while controlling for differences in broadleaf cover and elevation. We addressed three major questions for faunal diversity (species richness, Shannon and Simpson species diversity indices, species richness of guilds, and assemblage composition) in tree crowns: (1) does faunal diversity in a tree crown increase with increasing canopy density (*resource concentration hypothesis*) or (2) with increasing canopy heterogeneity (*habitat heterogeneity hypothesis*), and (3) do these relationships differ at the tree scale and stand scale?

2. Materials and methods

2.1. Study area and sampling trees

Arthropod diversity in spruce tree crowns was sampled in 2008 in the Bohemian Forest, on the border between Germany and the Czech Republic (Röder et al., 2010). We selected 60 mature spruce trees with an age of 80–120 years and a diameter at breast height of 32–140 cm (mean: 54 cm). Trees were located within a zone of publicly available LiDAR coverage. The average height of the top 10th percentile of tallest trees in the study area was 21.0 m (SD = 4.6 m). The selection of only one host species, i.e., Norway Spruce (*P. abies*), enabled us to control as many confounding variables as possible beyond forest structure (Progar and Schowalter, 2002). All spruce trees grew at elevations of 465–1285 m a.s.l. on acidic soil of similar geology and on the west-exposed slope of the Bohemian Forest. The minimum distance between sampled trees was 200 m, which has been shown to be sufficient to achieve spatial independence of capture rates for flight-interception trap samples (Müller and Brandl, 2009).

Norway Spruce is naturally dominant at elevations above 1150 m a.s.l., with only minor proportions of Mountain Ash [*Sorbus aucuparia* (L.)] and Sycamore Maple [*Acer pseudoplatanus* (L.)] defying the harsh conditions at these elevations (Bässler et al., 2010). At the lower elevations, our sampled stands were the product of historic alteration of tree species composition by modern forestry around the year 1900. The most important naturally admixed species with spruce in the area are European Beech (*Fagus sylvatica*), Silver Fir (*Abies alba*), and in some areas Scots Pine (*Pinus sylvestris*). The latter two species are also hosts of conifer-specialist insects that occur on spruce (Böhme, 2001). The herb layer varied between zero and 100% coverage in the stands.

2.2. LiDAR variables and covariates

Discrete-return LiDAR data were acquired in leaf-off periods between April 2008 and November 2009 using an airborne Riegl LMS-Q560 system (RIEGL Inc., Horn, Austria). The sensor operated at a wavelength of 1550 nm and scan angle of 60° and recorded the first and last return points. The average flight height above ground was 776 m, at an altitude of 1194–2306 m a.s.l., depending on topography, and an average flight speed of 55 m s⁻¹. As a result, we obtained a mean swath width of 832 m, a mean footprint diameter of 38.8 cm, and an average point density of 9.8 points m⁻², with a vertical error below 0.16 cm.

LiDAR data consisted of coordinates and height a.s.l. and was classified into ground and vegetation returns. Ground and

vegetation points were classified using TerraScan software (TerraSolid Ltd., Finland), which classifies ground points by iterative algorithms, generating a triangulated surface model. The data included a digital terrain model (DTM) in 1×1 m resolution calculated using SCOP++ with ‘adaptable prediction’ as an interpolation method. The DTM was used to calculate the above-ground height of each vegetation return. The vegetation height was calculated by subtracting the height of the underlying DTM from the height of each vegetation return. We only used vegetation returns having above-ground heights taller than 0.5 m because of possible errors from vertical inaccuracy in the LiDAR data or classification error. From the valid subset of data, we calculated vertical profile metrics of the maximum, mean, median, standard deviation, and coefficient of variation of vegetation heights within each cell of a systematic 5×5 m grid applied to the whole area. For each of these measures (except the coefficient of variation), we then calculated spatial averages and standard deviations for the vertical LiDAR metrics at two spatial scales. First, at the tree scale, we included 5×5 m grids within a radius of 10 m around each tree (average cell number of 12). This area well represents the crown architecture of the sampling tree itself, and its direct environment driven by the neighboring trees. Second, for describing forest structure at the stand scale, we selected all 5×5 m grid cells which were located with their center within a radius of 100 m (average cell number of 388) around the sampling tree.

Although leaf-off campaigns have been successfully used for modeling of forest species in past studies (Zellweger et al., 2013), they have the ecological consequence that broadleaf trees in winter (mostly European Beech in our study area) are penetrated by many more LiDAR pulses than would be the case after leaf flush (when insect sampling occurred). To avoid any potential bias that differing proportions of broadleaf trees across sites might introduce into our measures of canopy density and heterogeneity, we did not use any predictor variables for LiDAR penetration rate (see Müller and Brandl, 2009) or proportional canopy density measures (percentage of vegetation returns in certain canopy strata). We therefore used only the distribution of vegetation returns. In doing so, even 5×5 m grids dominated by broadleaf trees had vegetation return distributions that were strongly representative of the local distribution of biomass (wood and leaves), despite a lower absolute number of returns compared with spruce cells. Moreover, tree crowns of our mature beech and spruce trees regularly occupy areas larger than a single 5×5 m cell, therefore most individual cells are either pure spruce or beech cells (rather than mixed species). We summarized the calculated values for cells at the two spatial scales around each sampling tree. In that way we were able to remove the effect of higher absolute penetration rates in broadleaf trees in winter. This is confirmed by a lack of correlation of broadleaf tree proportion and canopy return measures after this selection (Fig. S1–3).

Because the various LiDAR-derived variables were typically intercorrelated, we ran principal components analyses (PCAs; one at the tree scale and one at the stand scale, separately) in an attempt to derive orthogonal measures of canopy resource availability versus canopy structural heterogeneity. In both PCAs, the loading of LiDAR variables on the first axis was dominated by the average height values (max_avg, hmean_avg, and h50_avg; Table S1). These values are highly correlated with the growing stock of stands (Nelson et al., 1988). We had no inventory data at hand for our spruce plots, but from a previous leaf-on campaign we could show that the growing stock of trees and mean height were highly correlated at the stand scale ($R^2 = 0.73$, $n = 288$; Müller and Brandl, 2009). Also Clawges et al. (2008) used LiDAR returns as a rough measure of the density of vegetation material. Thus, we considered that the use of PCA axis 1 as a surrogate for resource availability was justified (see also Clawges et al., 2008). The loading

of LiDAR variables on the second axis was dominated by vertical heterogeneity variables (max_sd, hmean_sd, h50_sd; Figs. S4–S7; Table S1). Therefore we use this axis as a surrogate for habitat heterogeneity that is independent of resource amount (Vierling et al., 2008). In the following analyses, we refer to these orthogonal gradients of canopy architecture as ‘Resource’ and ‘Heterogeneity’, respectively, at the tree and stand scales.

Beyond the variables derived from airborne LiDAR, we used two potential covariates of arthropod diversity patterns. First, we visually estimated the proportion of broadleaf tree cover at the stand level (radius 100 m), because broadleaf trees may provide important complementary habitats for species that might also occur in spruce canopies as tourists (Brändle and Brandl, 2001). Cover was estimated separately for the regeneration layer, the shrub layer and the tree layer, and the values were then summed. Finally, we took the elevation of each sampling tree from the terrain model. Elevation has been confirmed as an important surrogate for many ecologically important variables influencing arthropod diversity and distribution, including temperature and precipitation (Hodkinson, 2005). Of course, there are many other possible environmental covariates. However, with regard to limitations on statistical power with only 60 trees sampled, we selected the two variables (elevation and proportion of broadleaf trees) that have previously been found to be of relevance to arthropod diversity in our study area (Müller et al., 2010; Röder et al., 2010).

3. Arthropod sampling

One flight-interception trap was placed in each of the 60 spruce trees just prior to snow melt, between 20 March and 10 April 2008. Traps were positioned in the center of the green tree crown with the aid of a crossbow. The traps consisted of a crossed pair of transparent plastic intercept surfaces (40×60 cm) with a funnel of smooth plastic material attached to the bottom and a plastic roof at the top. To attract species searching for flowers, a yellow adhesive tape was applied to one of the intercept surfaces. At the end of the funnel, a 1-l sampling jar filled with killing and preserving agent (1.5% copper vitriol) was mounted. The traps operated during the whole growth period of 5–6 months and were emptied each month. Such window traps have been criticized for their limited ability to represent the localized fauna of an area, because they are open trap systems. However, ordination analysis of window-trap samples from different tree species (including spruce and beech) showed a strong ability to discriminate insect communities based on tree species identity (Gossner, 2008). All beetles (Coleoptera); true bugs, leafhoppers, and planthoppers (Hemiptera: Heteroptera, Auchenorrhyncha); lacewings and snakeflies (Neuropteroidea: Neuroptera, Raphidioptera); spiders and harvestmen (Arachnida: Araneae, Opiliones); and bees and wasps (Hymenoptera: Aculeata) were counted and determined to the species level.

According to the size-grain hypothesis (Kaspari and Weiser, 1999), small species perceive their environment as more rugose, particularly on plant surfaces that have been shown to have a high fractal dimension (Morse et al., 1985). Furthermore larger flying species are in general better dispersers (Gossner and Müller, 2011). Therefore, we expected the responses of small arthropods (classified as <4 mm in body length; 191 species; Gossner and Müller, 2011) to be greater at finer spatial scales. Moreover, all species were classified according to their major feeding preferences as carnivores, herbivores, fungivores, saprophages, or necrophages (for details, see Röder et al., 2010). To highlight tree-specific differences in herbivore foraging, we further separated the herbivores into two groups: xylophages (i.e., those species feeding on phloem and wood) and phytophages (i.e., those feeding on green tissues).

Furthermore, we classified members of the two dominant insect groups Coleoptera and Heteroptera into two categories of host specialization (conifer specialists or generalists), with a focus on our sampled tree species. Then, we counted the number of bark beetle species (Curculionidae, Scolytinae) assessed as pest species in Europe according to [Bussler et al. \(2011\)](#).

4. Statistical analysis

We verified the degree to which our estimates of species richness might be influenced by undersampling bias using two approaches (for more methodological details see [Appendix 4, Supplementary material](#)). First, we used a sample-size-based rarefaction approach to estimate the rate of increase in species richness with increasing number of trees sampled, and then extrapolated the observed accumulation curve using the recently developed analytical rarefaction-extrapolation approach of [Colwell et al. \(2012\)](#). Second, we also estimated accumulation rates in relation to the degree of completeness of sampling effort, rather than just sample size, as recently recommended by [Chao and Jost \(2012\)](#).

Sample coverage is considered to be an objective measure of sample completeness. One way to interpret sampling completeness in this sense is as the coverage deficit ($1 - \text{sample coverage}$), which represents the probability that the next individual collected belongs to a species not previously collected in the sample ([Chao and Jost, 2012](#)). Based on the estimated sample completeness, we projected the coverage-based rarefaction and extrapolation up to a maximum coverage, i.e., the coverage corresponding to a doubling of the number of trees actually sampled. All estimates, confidence intervals and plots were obtained using the software iNEXT (interpolation/extrapolation) available on-line at <http://chao.s-tat.nthu.edu.tw/inext/>. Although it is statistically difficult to accurately extrapolate to an infinite size (or a complete coverage), we can obtain a reliable lower bound of the asymptote (the true species richness) with a confidence interval based on the Chao2 estimator [see [Gotelli and Chao \(2013\)](#) for a review].

To extract a species composition component as a vector from our data we ran a Nonmetric Multidimensional Scaling (NMDS) ordination on Hellinger-transformed abundance data. From the ordination plot ([Fig. 2](#)) we selected one point as reference point and extracted the distance (i.e. community dissimilarity) to all other plots as an assemblage composition component from the distance matrix in further analysis. For beta-diversity patterns analyzed on a wider-scale survey across sites see [Röder et al. \(2010\)](#).

Finally, to test the independent effects of canopy resource density and canopy habitat heterogeneity at the tree scale vs. stand scale, while controlling for elevation and the proportion of broadleaf trees in the surrounding stand, we fitted multiple linear models in R 2.15.2 (www.r-project.org) and conducted backward selection of model parameters based on comparison of Akaike information criterion (AIC) values using the function *stepAIC* in the add-on package *mass*. Total abundance, total species richness and the richness of species per subgroup were $\log_{10}(x + 1)$ trans-

formed to meet model assumptions of normality and homogeneity of variances. To accurately reflect the scatter of partial correlations, we used partial regression plots ([Moya-Larano and Corcobado, 2008](#)). Based on previous studies and the distance between our sampling trees, we assumed spatial independence of the residuals ([Müller and Brandl, 2009](#)), which is a key assumption in multiple regression models ([Quinn and Keough, 2002](#)). For confirmation, we used the *spline.correlog* function (with 999 replications) in the *ncf* package in R2.13.1 ([Bjornstad and Falck, 2001](#)). Here, a 95% confidence limit for Moran's similarity indicates whether the model residuals are significantly more or less similar than expected by chance alone at any given spatial scale.

5. Results

From 10,080 trap-days sampling effort across 60 Norway Spruce trees, we collected 21,561 arthropods and classified them to species level, with 391 species identified within the 7 selected target taxa ([Tables 1 and S2](#)). Sample-size-based species accumulation curves ([Fig. 1a](#)) indicated that the fauna susceptible to capture by flight intercept traps was reasonably well sampled, but did not represent a complete census of species. An extrapolated estimate of species richness at twice the sampling effort (i.e., 120 trees) suggested that there would be >504 species (on average) at the site ([Fig. 1a](#)). The majority of these unsampled species are likely to be rare (and potentially vagrants in the canopy) as coverage-based rarefaction revealed high sample completeness (93.7%) from our sample of 60 trees ([Fig. 1b](#)). This indicated a relatively low coverage deficit, with only a 6.3% chance that the next individual sampled at random will be from a species not previously sampled. A sample completeness curve ([Fig. 1c](#)) showed that when sample size is increased from 60 to 120 trees, sample completeness increased from 93.7% to 96.8%.

The NMDS ordination of species composition showed site separation along the first axis which was strongly related to an axis of variation in elevation and canopy architecture in a post hoc fit of environmental variables (but was unrelated to proportion broadleaf cover) ([Fig. 2](#)). Our partial regression models ([Fig. 3](#)) showed significant influences of both canopy density and canopy vegetation heterogeneity on all measures of canopy arthropod diversity, after accounting for potential confounding variation in elevation or proportion of broadleaf tree cover ([Fig. 3](#)), with one exception. Total abundance was not correlated significantly with any of our predictors. None of the models showed spatial autocorrelation among sampling locations ([Fig. S8](#)). Of the covariables in the models, elevation had an unexpectedly weak relative effect on diversity variables, having only a small positive influence on the richness of xylophages and conifer specialists ([Fig. 3](#)). However, it had a strong effect on the species composition component ([Fig. 3](#)). By contrast, the proportion of broadleaf trees had a positive effect on all response variables except carnivore richness (e.g., [Fig. 4a](#)), with particularly strong effects on the richness of phyllophages and xylophages ([Fig. 3](#)).

Table 1
Summary of the number of species recorded in each of the selected target taxa, as well as the numbers of species in each designated feeding guild and host specialization category. For a full list of species, see [Table S2](#).

Taxa	Species	Feeding guild	Species	Conifer specialization	Species
Aculeata	24	Carnivores	197	Specialists	101
Araneae	35	Fungivores	37	Generalists	200
Auchenorrhyncha	15	Phyllophages	78	Not classified	93
Coleoptera	270	Xylophages	72		
Heteroptera	31	Saprophages	6		
Neuropteroidea	17	Necrophages	4		
Opiliones	2				

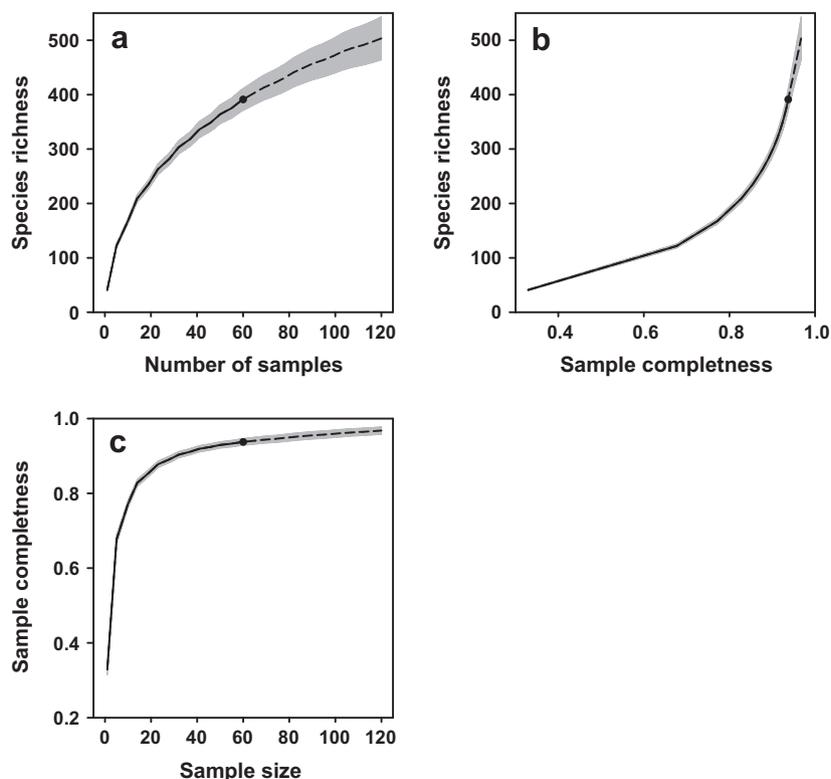


Fig. 1. (a) Sample-size-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the sample size actually taken) of arthropod species richness, along with 95% unconditional confidence intervals (gray shading). The black dot indicates the full sampling extent in this study (60 trees). (b) Coverage-based rarefaction (solid line) and extrapolation (dashed line) with 95% unconditional confidence intervals. The black dot indicates the full sampling extent in this study. The coverage is extrapolated from the current sample (93.7%) to 96.8% (i.e., the coverage value for a doubling of the original sample size). (c) The sample-completeness plot with 95% confidence interval for rarefied samples (solid line) and extrapolated samples (dashed line) as a function of the number of trees. All 95% confidence intervals in three panels were obtained by a bootstrap method based on 200 replications (Chao and Jost, 2012).

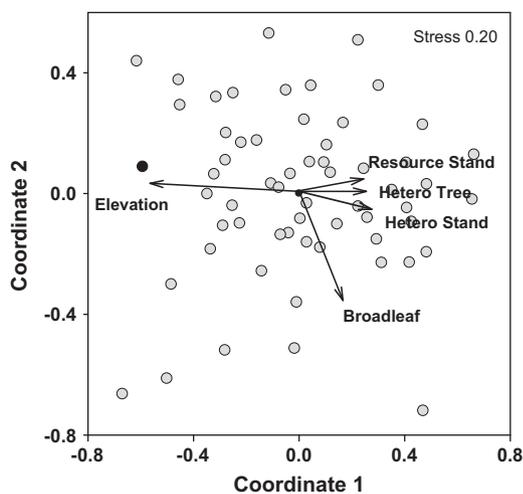


Fig. 2. Ordination plot of a Nonmetric Multidimensional Scaling (NMDS) for species-abundance data after Hellinger transformation. Correlations with measured environmental variables were fitted post hoc to the ordination (only variables with $p < 0.05$ are shown). The black marked site was arbitrarily selected as a reference point to calculate a vector of assemblage dissimilarity.

With respect to the overall model fit the richness of larger species could be slightly better explained than for smaller species, but for the latter tree level variables were more important (Fig. 3). Although the overall explanatory power of some models was low, particularly for fungivore richness (Fig. 3), the models explained 26–53% of variation in total species richness, diversity

and assemblage composition across sites (Figs. 3 and 4). Surprisingly, the relative influence of vegetation structure on arthropod diversity varied dramatically across two scales. At the tree scale, both canopy density (e.g., Fig. 4b) and canopy heterogeneity (e.g., Fig. 4c) had positive influences on arthropod species richness, but these effects were typically stronger for heterogeneity (Fig. 3). There were only weak positive tree-scale effects of canopy density for seven of the ten dependent variables, and surprisingly no significant relationship with phyllophage richness or the richness of conifer specialists (Fig. 3). By contrast, the stand-scale effects of canopy density were strong, and negative, in all models except fungivore richness (Fig. 3). This indicated that more open stands with higher broadleaf tree cover and lower canopy density of conifer trees typically had greater canopy arthropod diversity, even of conifer specialists (Fig. 3). The contrast between positive tree-scale effects but negative stand-scale effects of canopy vegetation density on arthropod diversity is striking, especially given the broad positive correlation in vegetation structural measures across spatial scales at the 60 sampling sites (Fig. S1). This clearly highlights the need to partition the relative responses of canopy arthropods to habitat structure at multiple spatial scales.

6. Discussion

We found strong context dependence in the response of canopy arthropod communities to the three-dimensional architecture of Norway Spruce canopies. At the two spatial scales most relevant for forest management—the tree scale and stand scale—vegetation density and vegetation heterogeneity had contrasting influences on all measures of biological response, from assemblage

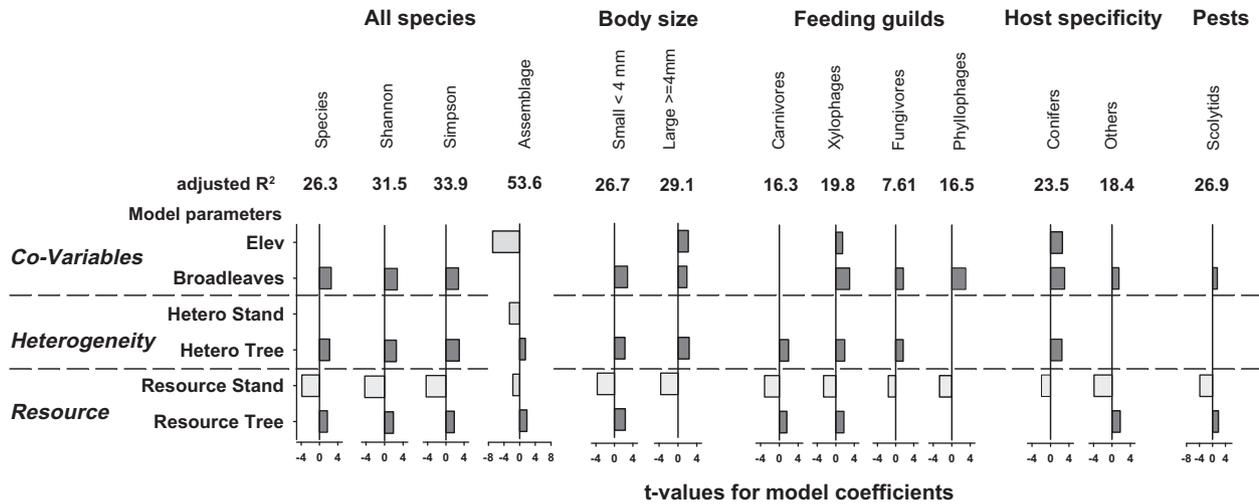


Fig. 3. Significance and direction of effect (*t*-values) for model coefficients in multiple regression models, following backward step-wise model selection using Akaike information criterion (AIC). Dark gray shading denotes significant positive predictors; light gray shading denotes significant negative predictors. Note that Total Abundance was also tested as a response variable, but no significant variation was explained by the predictors.

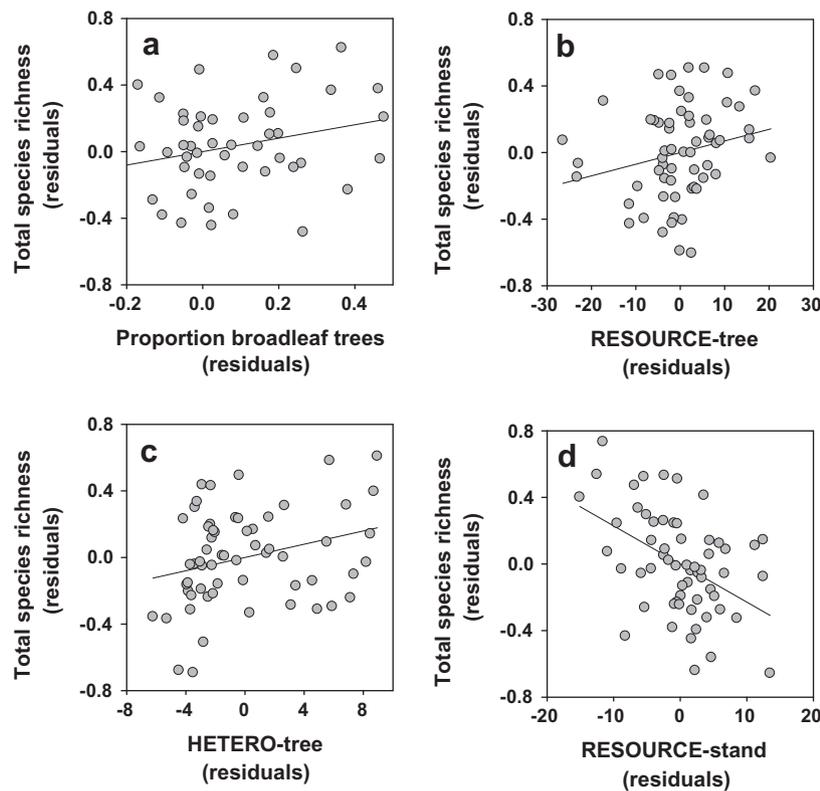


Fig. 4. Partial regression plots of the effects of vegetation structure on canopy arthropod species richness (i.e., the residual of Y on the remaining explanatory variables vs. residuals of the target explanatory variable on the remaining explanatory variables) for the four predictor variables selected in the final regression model for total species richness ('Species' in Fig. 2).

composition to taxonomic richness to feeding guild proportionality and degree of host specialization. At the tree scale, individual tree crowns with high vegetation density and high structural heterogeneity promoted a correspondingly high diversity of canopy arthropods, whereas the reverse was true at the stand scale. More open forest stand structure with lower conifer density and a high proportion of broadleaf trees actually promoted increased stand-level arthropod diversity, irrespective of patterns of stand-level heterogeneity. These findings suggest that quantifying forest architecture

at tree and stand scales greatly improves understanding of the drivers of species richness within tree crowns (Ishii et al., 2004).

Our results demonstrated that even in montane areas, where tree diversity is relatively low and forests have historically been subject to management disturbances associated with timber harvesting, there can still be high arthropod biodiversity values worth conserving. Our arthropod sampling over the course of a full growing season revealed a high diversity of 391 species in just 7 target groups, with relatively high sample completeness (and low

coverage deficit) compared to other biodiversity studies (Chao and Jost, 2012; Colwell et al., 2012). We estimated that if we were to double our sampling effort to 120 trees, possibly 470–536 species (with sample completeness of 96.8%) would be found at our study site. A lower bound of species richness (the asymptote of the extrapolation curve) based on the Chao2 estimator is 623, with a 95% confidence interval of 541–748. This implies that if we could conduct a complete census, the species richness would be at least 623. Our estimate of 470–536 species corresponds closely to the 555 species identified in the broader study of Röder et al. (2010), which comprised twice the number of traps as used in our LiDAR application. Our estimate is perhaps lower than that observed empirically because Röder et al. (2010) sampled at lower elevations across a broader range of geography and tree diversity in the Czech Republic (see map in Röder et al., 2010), which will inevitably lead to higher beta diversity among samples.

In contrast to what might be predicted from the resource concentration hypothesis, dense spruce forest stands with high canopy volume and a large quantity of leaf resources do not appear to promote biodiversity within individual spruce crowns. In fact, the effect was clearly the reverse, with diversity increasing with decreasing vegetation resource availability. This is also in contrast to findings for nocturnally active insects sampled in light traps, where vegetation density was partly measured using LiDAR techniques (Müller et al., 2012). Given that such light traps have been shown to mirror local assemblage composition quite well at an attraction distance of up to 30 m (see Müller et al., 2011), they can therefore be compared directly to our results at the stand scale. For instance, both Ober and Hayes (2008) and Müller et al. (2012) reported increasing local abundance and richness of moths and flies with increasing stand density. These contrasting results might be explained by a general difference in the resource use of nocturnal and diurnal arthropods (most of our sampled species were known to be diurnally active). For diurnal arthropods, the availability of sunlight might be more important than vegetation resources, particularly in montane forests, and from this perspective, solar radiation in open stands and not leaf area per se may act as the critical resource leading to increasing densities there. There has also been debate about the degree to which flight trap catches are more representative of the activity of insects, rather than local densities. This certainly may affect trap locations with very different microclimatic conditions. In our study all traps were set up in the center of spruce crowns. Therefore we are confident that potential differences due to differing solar radiation at the trap location are not a confounding issue affecting our results.

It seems more probable that variation in response to forest structure (vegetation resources) is a result of fundamental differences in life history strategies among different lineages. For near-ground communities in the same study area, contrasting taxon-specific responses to canopy density have already been demonstrated. For example, bees and syrphid flies showed higher richness in open stands with low canopy density, whereas mollusks and fungi had higher richness in closed stands (Lehnert et al., 2013). Similarly, the richness of different trophic feeding groups of beetles, such as fungivores and xylophages, showed different response to canopy cover (Müller et al., 2010). In general, the higher species richness and diversity of arthropod assemblages of spruce trees in stands with lower canopy density is mostly in line with previous findings for ground-dwelling spiders or beetles at the stand level (Müller and Brandl, 2009; Vierling et al., 2011). In our study also the assemblage composition component was affected independently from elevation by all architectural variables, which also supports the view that different species occur in different canopy structures (Fig. 3). These contrasting responses of species to different canopy architecture at different strata underlines the importance of considering a broad array of taxa and strata, as well as

different successional stages, to fully understand the relationship between biodiversity and resource distribution in forests (see Swanson et al., 2011; Basset et al., 2012).

The effects of local vegetation structure within individual tree crowns on arthropod diversity at the tree scale strikingly differed from those at the stand scale. At the tree scale, both resource concentration and habitat heterogeneity had complementary positive influences on arthropod diversity. For many species, the absolute quantity of resources such as twigs or leaves may have a strong influence on feeding or foraging habitat. For example, it has been shown that experimental reduction of needles and branches reduces the diversity of a predatory spider guild, and that species respond differently depending on their foraging strategy (Halaj et al., 2000). For herbivores such as caterpillars, the availability of conifer needles is a critical determinant of population abundance and species richness (Schowalter et al., 1986).

The additional influence of tree-scale heterogeneity on faunal diversity strengthens the view that tall-crowned trees (represented by high tree-scale heterogeneity) support a greater variability in microclimate and microhabitat niches, leading to higher local diversity. Such an influence of plant architecture on phytophages has been considered one of the classical determinants of insect-plant relationships (Lawton, 1983; Strong et al., 1984), and yet phyllophage diversity was one of our few response variables that was unaffected by tree-scale variation in either resource availability or vegetation heterogeneity. It might be that from the perspective of phyllophages the amount (resource) and variability (heterogeneity) of the distribution of green needles at the tree level is of lower importance, because the high abundance of spruce at the landscape scale provides a rather homogeneous distribution of available hosts for phyllophages (Röder et al., 2010), resulting in quite similar richness values in different trees. By contrast, other feeding guilds seem to depend more on vegetation structure (such as spiders requiring a substrate for building their webs, or saproxylic beetles requiring a specific moisture content and diameter of wood), which leads to higher tree-scale dependence. Moreover, habitat conditions beyond the plant species have also been shown to be an important driver for monophagous insects on trees, such as nocturnal moths (Müller et al., 2011).

We expected that the richness of smaller-bodied species would respond more to local (tree-scale) variability of vegetation structure than the richness of larger-bodied species. This was only partly supported, as the richness of both small- and large-bodied species followed a similar overall trend, but with a slight indication of a more fine-scale response for smaller species (see Fig. 3). Of course, from the perspective of insects <4 mm in size, the scale of our study was still very coarse, and much higher resolution measurements of crown and needle structure would inevitably be required to gain a deeper understanding of the fractal dimensions of trees as habitats. For this, combining terrestrial and airborne LiDAR campaigns may open up the required resolution of very fine canopy structures, as it has recently proven to be useful in measuring fine twig structures (Bayer et al., 2013). Our understanding of fractal dimensions of trees may progress with correlation of canopy fogging data from single trees with terrestrial scans and airborne LiDAR scans (Weibel, 1991).

The spruce forests in our study system are characterized by frequent natural disturbance events, specifically through storms and bark beetle outbreaks (see Svoboda et al., 2012). Such disturbances, together with high snow cover in natural spruce forests, create naturally more open stands with emergent single trees with tall crowns than in, e.g., beech (*F. sylvatica*)-dominated forests, which are the second most important forest type in our study area and form a dense and more homogenous canopy (Packham et al., 2012). Even for broadleaf trees, large crown size and high canopy heterogeneity have been suggested as being the most important

drivers of species richness, and this is empirically supported by recent canopy fogging studies (Dolek et al., 2009). However, the relative roles that these variables play in determining the effects of canopy architecture on assemblage patterns have not been effectively discriminated. Future studies could benefit greatly from a LiDAR remote-sensing approach to measuring canopy architecture across a range of tree species and stand types, and associating this architecture with patterns of variation in faunal diversity.

In summary the major advantage of LiDAR is its great potential to measure vegetation complexity very precisely at fine spatial grain across broad spatial extents. This enables ecologists, forest managers, and conservation practitioners to link canopy biodiversity with architectural complexity at scales not previously achievable (Schowalter, 1995). Such links should also allow the incorporation of tree-crown biodiversity into single tree-based stand simulator models (Pretzsch et al., 2002). This example of such an approach here for spruce forests in the mountains of Europe indicated that a relatively low canopy density at the stand scale, with tall individual tree crowns and high local vertical heterogeneity around trees, is most favorable for the diversity of the canopy arthropods surveyed. Such results provide complementary knowledge of forest structure beyond tree species or dead wood for forest biodiversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.10.014>.

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